LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *PROCECIDOCHARES STONEI* BLANC & FOOTE ON *VIGUIERA* SPP. IN SOUTHERN CALIFORNIA (DIPTERA: TEPHRITIDAE)

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Abstract.—*Procecidochares stonei* Blanc & Foote is a facultatively multivoltine, stenophagous, gall-forming fruit fly on *Viguiera laciniata* Gray and *V. deltoidea* Gray var. *parishii* (Greene) Vasey and Rose (Asteraceae) in southern California. The latter host record is new; other published host records are questioned. Eggs, first through third instar larvae, and puparia are described for the first time. Galls formed on both host plants are described. The severe drought in southern California during the last 5 years has reduced the densities of *P. stonei* on *V. d.* var. *parishii.* Fly reproduction was restricted to one generation per year on the few host plant individuals that thrived in favored sites where they received supplemental water (i.e., along drip lines of boulders and margins of paved roads). Adult behaviors described include grooming, feeding, wing displays, courtship, copulation and oviposition. Females typically lay eggs in clusters of two or more in axillary buds. Larvae develop gregariously, mainly as two, but up to 13 per gall. Four species of hymenopterous parasitoids are reported, the most common of which was *Eurytoma* sp. (Eurytomidae).

Key Words.—Insecta, *Procecidochares, Viguiera,* gall, immature stages, larval morphology, mating behavior, parasitoids

This paper continues a series of life history studies on non-frugivorous species of Tephritidae (Diptera) native to southern California. *Procecidochares stonei* Blanc & Foote is one of several, little known species in this genus currently under study (Goeden, Headrick, & Teerink, unpublished data). It was previously known only from a taxonomic description of adults reared from galls on *Viguiera laciniata* Gray, and from a published biology, as well as host records that we believe instead apply to other species of *Procecidochares.* Adults of these species are morphologically and biologically similar, but differ in their host-plant associations and subsequently their gall morphology. These undescribed species have been (Silverman & Goeden 1980) or are currently under study; however, the present study based on biological data collected from the type locality distinguishes *P. stonei* from its related species, defines its host range, and resolves biological data from previously published reports.

MATERIALS AND METHODS

Galls in different stages of development were collected from plants at six different localities in southern California. Galls on *V. laciniata* were sampled at Otay Mesa and Otay Valley, in coastal, southwestern San Diego County. The Otay Mesa site is the type locality for the species, and overlooks San Ysidro just north of Tijuana, Mexico, at 45 m elevation. The Otay Valley site is nearby in San Ysidro at 35 m elevation on a south-facing roadside slope.

Galls on *V. deltoidea* Gray var. *parishii* (Greene) Vasey & Rose were sampled

at Oriflamme Canyon in eastern San Diego County, at Mountain Springs in southwest Imperial County, at Chino Canyon and along the Palms-to-Pines Highway above Palm Desert in Riverside County. Oriflamme Canyon is located at 665 m elevation, east of the Laguna Mountains, in a transition zone between the Colorado Desert and high chaparral. The Mountain Springs site is in a rocky area at 645 m, just north of the Mexican border; the Chino Canyon site is near the entrance to the Palm Springs Aerial Tramway, at 725 m elevation. The Palms-to-Pines Highway site is at 945 m above and west of Deep Canyon, on rocky, barren slopes.

Samples were returned to the laboratory, measured and dissected. More than 500 galls were dissected during this study. All larvae and 10 puparia dissected from these galls were preserved in 70% EtOH for scanning electron microscopy (SEM). Puparia were placed in separate glass rearing vials stoppered with absorbant cotton and held in humidity chambers for adult emergence. Specimens for SEM later were rehydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated with a gold-palladium alloy and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Up to 12 adults of each sex from each study site were point-mounted as vouchers for the research collection of RDG; vouchers of immature stages were placed in the collection of immature Tephritidae of DHH; reared parasites were placed in a separate collection of parasitic Hymenoptera associated with Tephritidae belonging to RDG. The description of immature stages follows the terminology and format defined by Headrick & Goeden (1990), including the modifications addressed by Headrick & Goeden (1991). Most adults reared from isolated puparia were individually caged in 850 ml, clear-plastic, screened-top cages fitted with a cotton wick and basal water reservoir and provisioned with a strip of yeast hydrolyzate and sucrose-impregnated paper toweling. The cages were used for longevity studies and oviposition trials.

Virgin male and female flies obtained from emergence vials were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton (Headrick & Goeden 1991) for direct observations, videotaping, and still-photography of their general behavior, courtship, and mating. Pairs were held together for at least 1 week, and observations were made throughout the day.

To quantify the effects of drought, galls were categorized as current-year's, last-year's, and previous-years' in a field survey at the Palms-to-Pines site in April, 1990, and gall abundance on 11 host plants was tabulated (Table 1). Each host plant was measured and diagramatically divided into four quadrants along compass coordinates, within which the position of each gall was noted.

Plant names follow Munz (1974); insect names, Foote & Blanc (1963). Means ± standard errors are reported herein.

Taxonomy

Procecidochares stonei Blanc & Foote

Egg.—Smooth, white, cylindrical, elongate, and tapered on both ends (Fig. 1A). Length 0.4–0.5 [0.5 ± 0.02] mm, width, 0.06–0.12 [0.08 ± 0.01] mm ($n = 5$). Apical end bears nipple-shaped pedicel with few aeropyles (Fig. 1B).

Table 1. Gall numbers and locations on 11 *Viguiera laciniata* plants at the Palms-to-Pines site in April 1990.

| | Galls sampled | | |
Quadrant	Previous years'	Last year's	Current year's
NW	99	6	2
NE	117	8	1
SW	86	15	5
SE	102	15	8
Totals	404	44	16

Third Instar Larva (fully grown).—White, barrel-shaped, tapered anteriorly, rounded posteriorly (Fig. 2A). Gnathocephalon conical, flattened dorsally, rounded lateroventrally; slightly protruding ventrally from prothorax (Fig. 2B), where it forms the mouth lumen at its anterioventral apex. Integument surrounding lumen rugose ventrally, with 4 smooth petals dorsally (Fig. 2B—1). Paired tridentate mouth hooks, directed ventrally (Fig. 2B—2), protrude from lumen. A laterally flattened median oral lobe lies between mouth hooks (Fig. 2B—3), with no ventral papilla (we were unable to see if it was attached basally to the labial lobe). Dorsad of mouth lumen, on anteriormost face of gnathocephalon, are paired anterior sensory lobes (Figs. 2B—4, 2C), each with flattened lobes bearing several sensory organs; a protruding, dome-shaped, dorsal sensory organ (Figs. 2B—5, 2C—1) is adjacent to dorsomedial apex of each anterior sensory organ. On dorsolateral margin of each lobe lies 1 small sensillum (Fig. 2C—2). Each anterior sensory lobe bears 1 lateral sensory organ (Fig. 2C—3), as a small, slightly raised papilla; a pit sensory organ (Fig. 2C—4), as a slightly raised area with an invagination on its surface; and a terminal sensory organ (Fig. 2C—5) of several papillae on a slightly raised area covering about 20% of the total lobe, not surrounded by a cuticular ring. A stomal sense organ (Fig. 2B—6) lies ventrolaterad of each anterior sensory lobe, and is located on gnathocephalon edge near the mouth lumen; each of these organs bears several small sensory papillae. Prothorax widens posteriorly (Fig. 2B—P); integument smooth, relatively featureless, but bears 1 row of flattened sensilla circumscribing its anterior margin. One pair of dorsolateral anterior thoracic spiracles on posterior margin of prothorax (Fig. 2D); each normally consists of 2 or 3, dome-like spiracular papillae each bearing a slit-like opening. Meso- and metathorax widen posteriorly, in similar appearance to abdominal segments. Typical abdominal segment bears a spiracular complex laterally along the midline (Fig. 2E); spiracles circular, do not protrude (Fig. 2E—1); each spiracular complex with dome-like sensillum anterior to its opening (Fig. 2E—2). Abdominal integument relatively smooth, featureless; abdominal segments I–III widen posteriorly, reach maximum width at segments IV–VI; segments VII and VIII narrow slightly, latter (caudal) bluntly rounded posteriorly, bearing posterior spiracular plates that bear 3 oval rimae with spiracular slits (Fig. 2F—1), an ecdysial scar (Fig. 2F—2) (found only on second and third instars), and thorn-like interspiracular processes on outer margins of each greatly reduced and often indistinct spiracular slit (Fig. 2F—3).

Second Instar Larva.—White, barrel-shaped, tapered anteriorly, rounded posteriorly (Fig. 3A). Mouth hooks tridentate (Fig. 3B—1), median oral lobe present (Fig. 3B—2). Prothorax bears anterior spiracles, each with 2 domed openings (Fig. 3C); lateral spiracles not observed; each posterior spiracular plate bears 3 rimae (Fig. 3D—1) and an ecdysial scar (Fig. 3D—2); interspiracular processes extremely small (Fig. 3D—3).

First Instar Larva.—White, barrel-shaped, tapered anteriorly, rounded posteriorly (Fig. 4A): differs from later instars with: mouthhooks bidentate (Fig. 4B—1); median oral lobe rounded anteriorly (Fig. 4B—2); anterior sensory lobes directly above mouth lumen, their sensilla much reduced, with only dorsal sensory organ (Fig. 4C—1) and terminal sensory organ (Fig. 4C—2) visible; anterior spiracles absent; no lateral spiracles observed; posterior spiracles reduced, their plates bear two indistinct oval rimae, each with no observable openings (Fig. 4D—1); interspiracular processes clearly visible, multibranched, and blade-like (Fig. 4D—2); no ecdysial scar present.

Puparium.—Black, barrel-shaped, gently tapering anteriorly, rounded posteriorly (Fig. 5A); 3.0–5.3 [4.2 ± 0.03] mm long (*n* = 180), 1.3–2.7 [1.9 ± 0.02] mm wide (*n* = 201). Most third instar larval structures retained in hardened and reduced state; gnathocephalon invaginated before pupariation, not visible (Fig. 5B). Posterior spiracular slits flattened, more sharply defined than in third instar (Fig. 5C—1); interspiracular processes reduced to barely distinguishable blemishes (Fig. 5C—2).
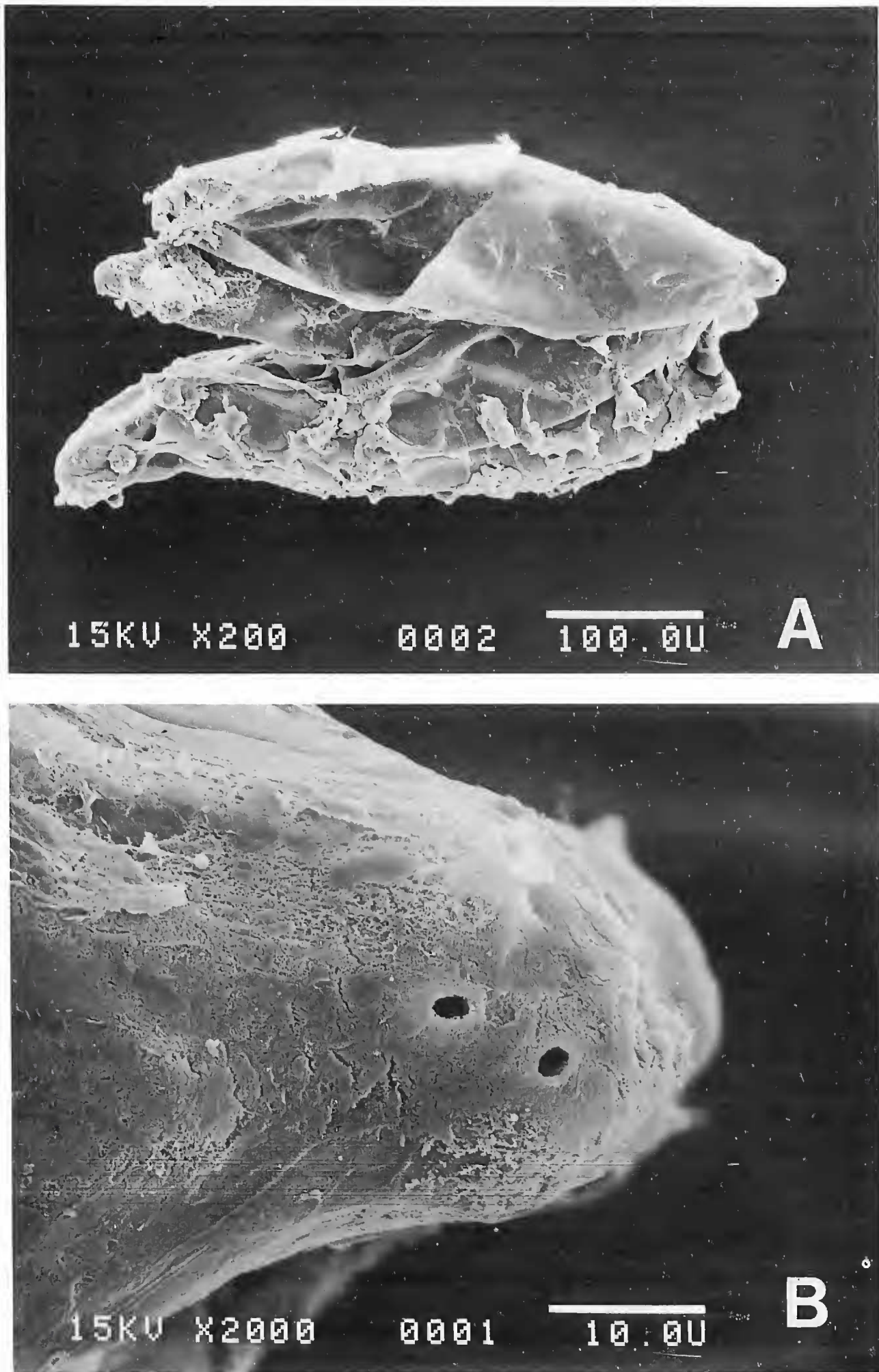
Figure 1. Egg of *Procecidochares stonei*: (A) cluster of three eggs; (B) detail of anterior end showing two aeropyles.
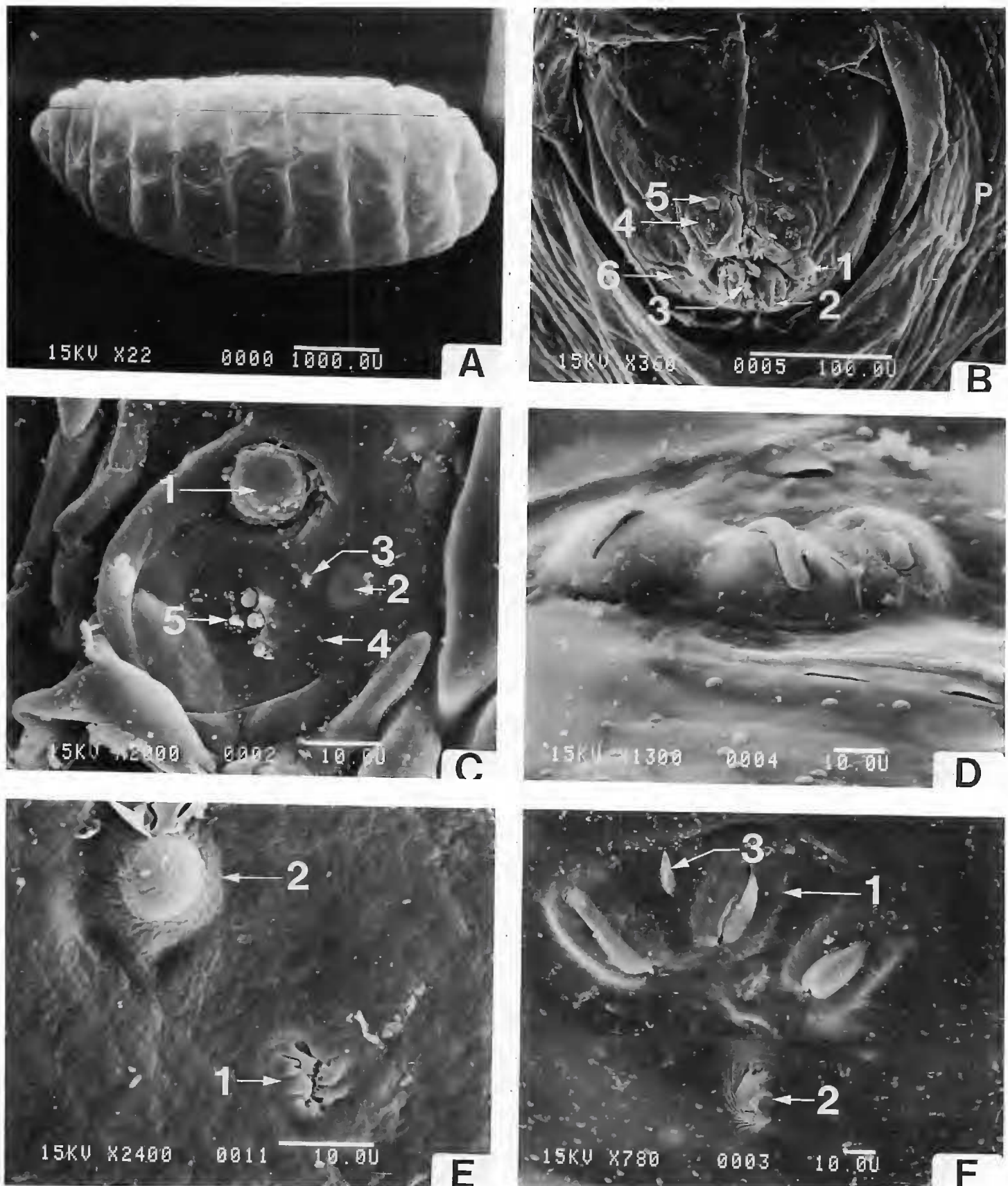
Figure 2. Third instar larva of *P. stonei*: (A) habitus, anterior to the left; (B) anterior view of gnathocephalon, 1—dorsal petals, 2—mouth hooks, 3—median oral lobe, 4—anterior sensory lobe, 5—dorsal sensory organ, 6—stomal sensory organ; (C) left anterior sensory lobe, 1—dorsal sensory organ, 2—sensillum, 3—lateral sensory organ, 4—pit sensory organ, 5—terminal sensory organ; (D) anterior spiracle; (E) lateral spiracular complex, 1—spiracle, 2—sensillum; (F) posterior spiracular plate, dorsal to right, 1—rima, 2—ecdysial scar, 3—interspiracular process.

Material Examined.—CALIFORNIA. *SAN DIEGO Co.*: San Ysidro, N of Tijuana, Mexico, 45 m, 27 Feb 1990, 12 Feb 1991, R. D. Goeden, *V. laciniata* Gray, galls containing immature stages.

BIOLOGY AND SEASONAL HISTORY

Gall.—Galls were collected from *V. laciniata,* the host plant at the type locality (Fig. 6A), and *V. deltoidea* var. *parishii,* a new host recorded here for the first
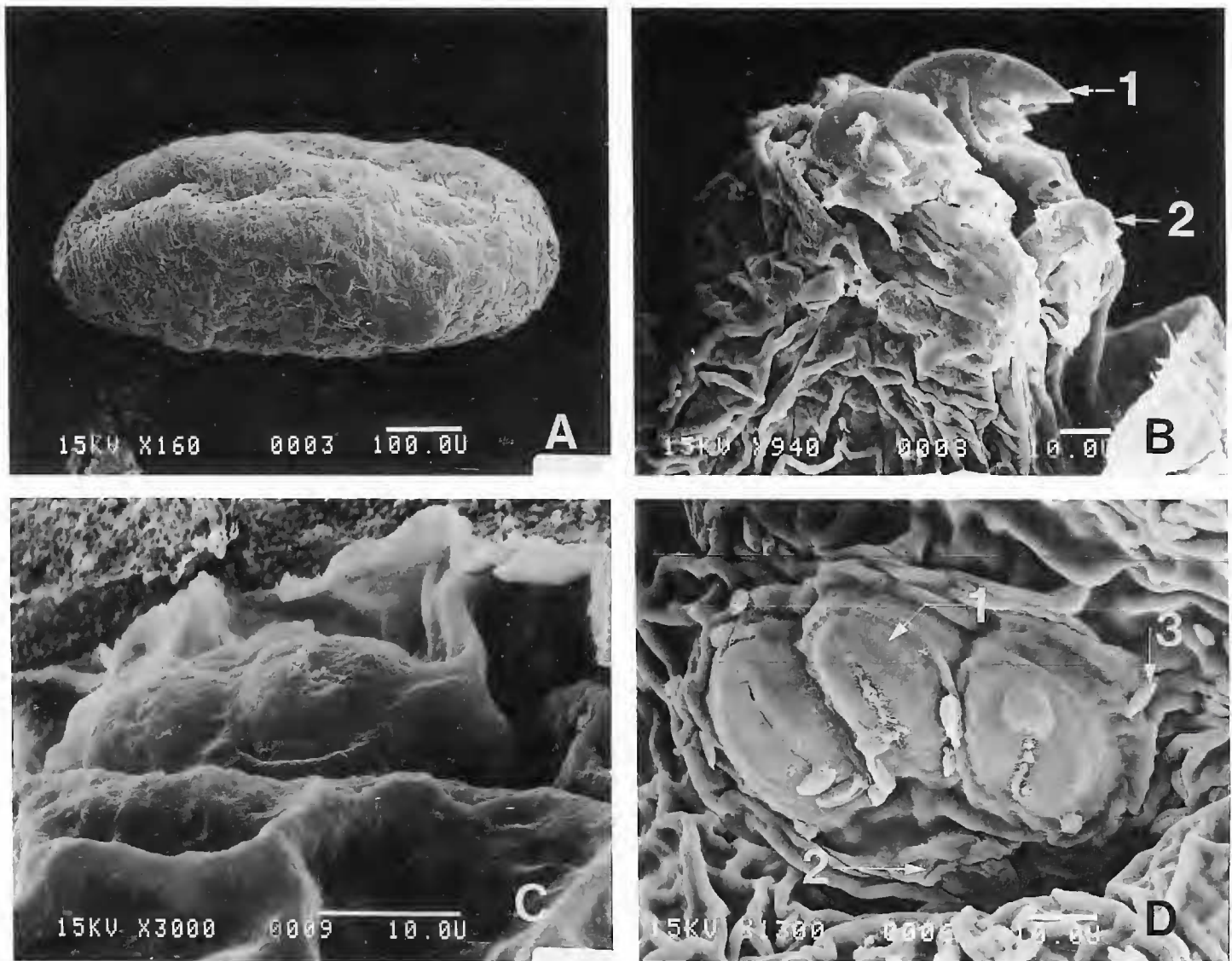
Figure 3.   Second instar larva of *P. stonei*: (A) habitus, anterior to left; (B) lateral view of gnathocephalon, 1—mouth hooks, 2—median oral lobe; (C) anterior spiracle; (D) posterior spiracular plate, dorsal to right, 1—rima, 2—ecdysial scar, 3—interspiracular process.

time (Fig. 6B). *Viguiera* are short, bushy, multibranched perennials with yellow flower heads in the tribe Heliantheae of the Asteraceae. In southern California, *V. laciniata* is found only in southern San Diego County on dry slopes below 760 m in coastal sage scrub and chaparral. *Viguiera d.* var. *parishii* is found in the Colorado and East Mojave Deserts in sandy canyons and mesas below 1520 m in creosote bush scrub (Shreve & Wiggins 1964, Munz 1974). The axillary bud galls of *P. stonei* were found on the lower portions of previous growing season's branches of both host species. They lack or have short pedicels, and are dark green, subspheroidal, and bear many bract-like leaves, especially apically (Fig. 6B).

Several features were measured on mature galls containing puparia from both host species. Galls from *V. laciniata* measured 2.9–12.5 [7.9 ± 0.25] mm in width and 3.9–15.2 [9.5 ± 0.3] in length ($n = 80$). Galls from *V. d.* var *parishii* measured 2.9–13.8 [7.1 ± 0.16] mm in width and 3.2–18.27 [8.8 ± 0.25] mm in length ($n = 149$). These means were not significantly different (t-statistic width = 1.27, length = 1.61; df = 227; $P = 0.025$). The single cavity within galls of *V. laciniata* measured 1.49–8.1 [4.5 ± 0.13] mm in width, and 2.8–9.9 [6.1 ± 0.18] mm in length ($n = 80$). Each cavity in galls from *V. d.* var. *parishii* measured 2.0–11.2 [4.76 ± 0.12] mm in width and 2.0–11.18 [5.9 ± 0.14] mm in length ($n = 149$).
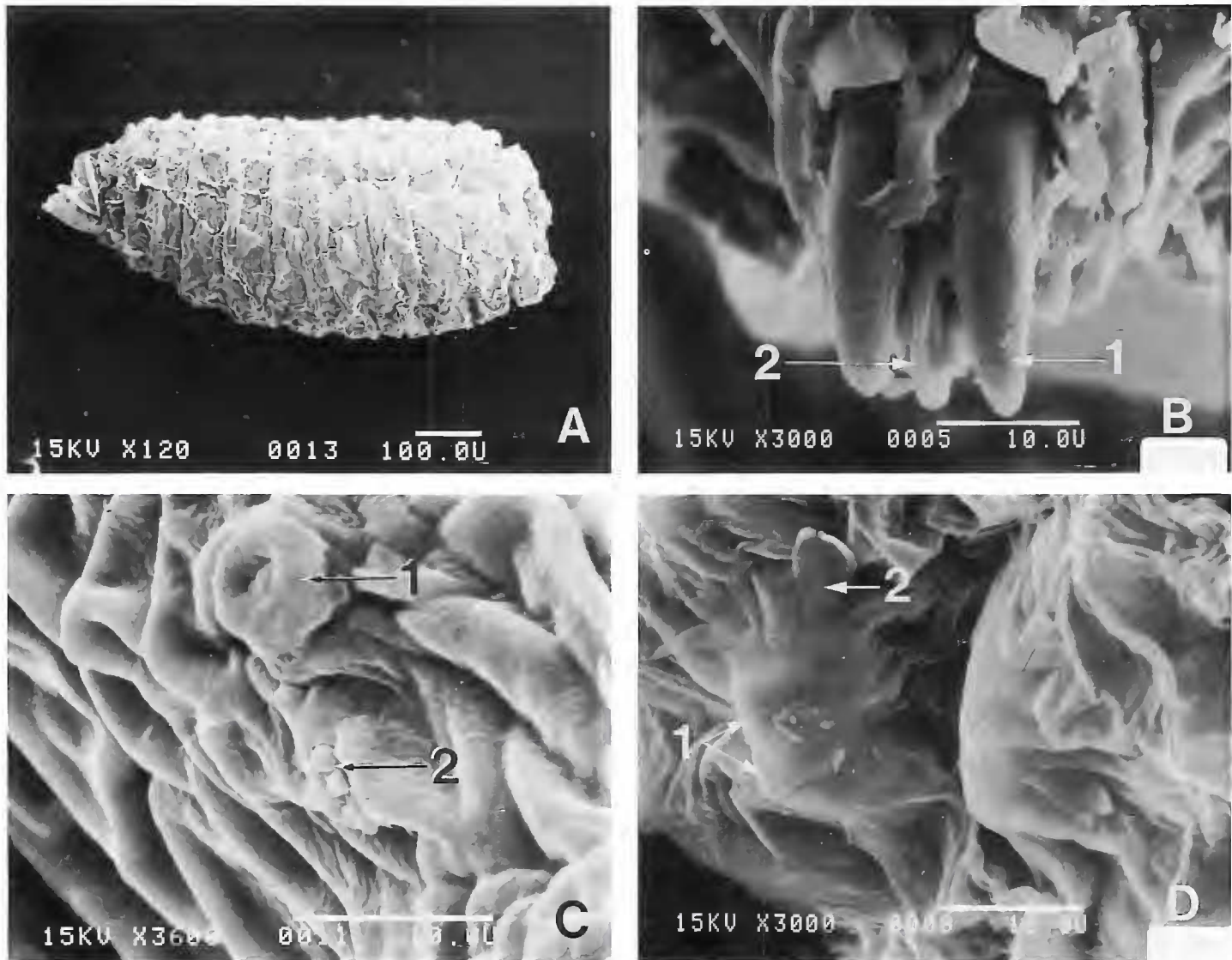
Figure 4. First instar larva of *P. stonei*: (A) habitus, anterior to left; (B) anterior view of mouth, 1—mouth hooks, 2—median oral lobe; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ; (D) posterior spiracular plates, dorsal end up, 1—rimae, 2—interspiracular processes.

Again, these means for cavity sizes were not significantly different (*t*-statistic width = 1.75, length = 0.69; df = 227; *P* = 0.025).

Procecidochares stonei larvae develop gregariously within a gall. The number of individuals per gall on *V. laciniata* was 1 to 13 averaging 2.5 ± 0.1 (*n* = 309), and on *V. d.* var. *parishii* was 1 to 3 averaging 1.4 ± 0.04 (*n* = 192); these means were significantly different (*t*-statistic = 7.7; df = 489; *P* = 0.025).

Egg.—Females begin to oviposit eggs, usually in clusters of two or more, shortly after their emergence in mid-spring (i.e., late March though April). Eggs are inserted into the axil between a branch and the base of a leaf petiole on the new growth (Fig. 6C).

Larvae.—First instar larvae eclose shortly after oviposition and begin to feed head-down in an axillary bud. The larva inhibits axillary branch elongation and induces thickening (Fig. 6D). First instar larvae aestivate in the small, incipient

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Figure 5. Puparium of *P. stonei*: (A) habitus, dorsal view, anterior to left; (B) anterior end, arrow denotes right anterior spiracle; (C) posterior spiracular plate, dorsum to right, 1—spiracular slit, 2—interspiracular process.
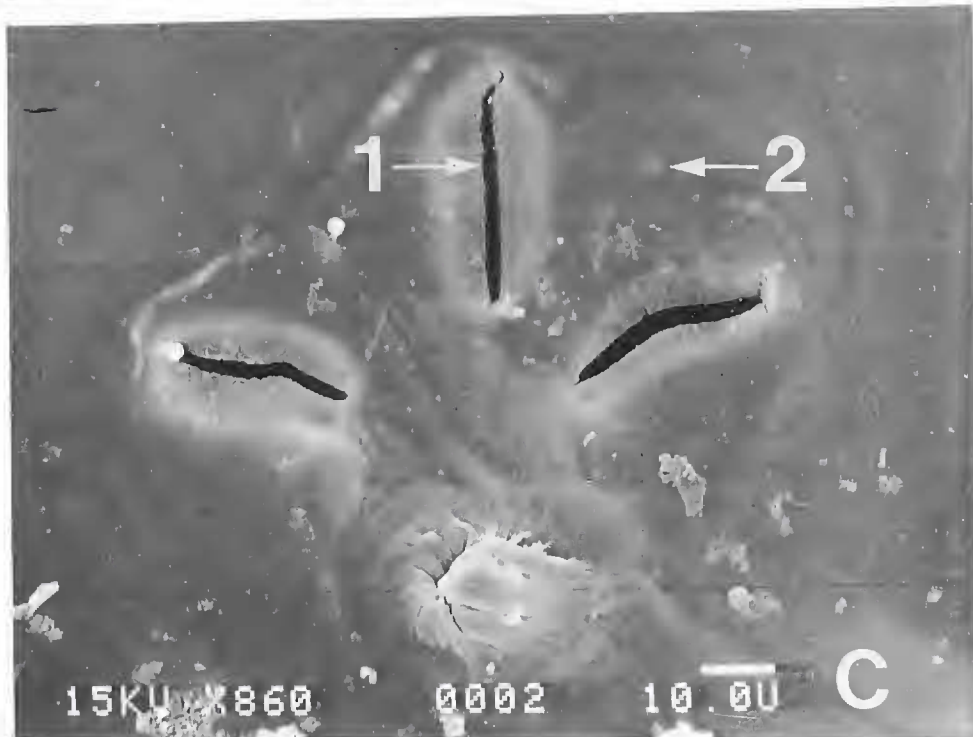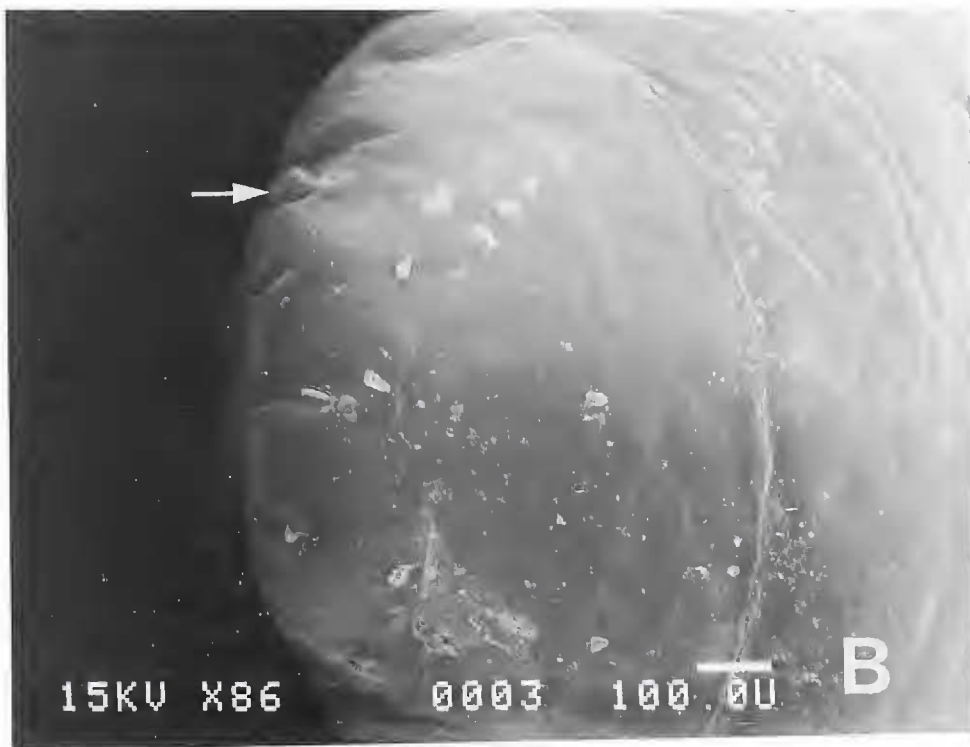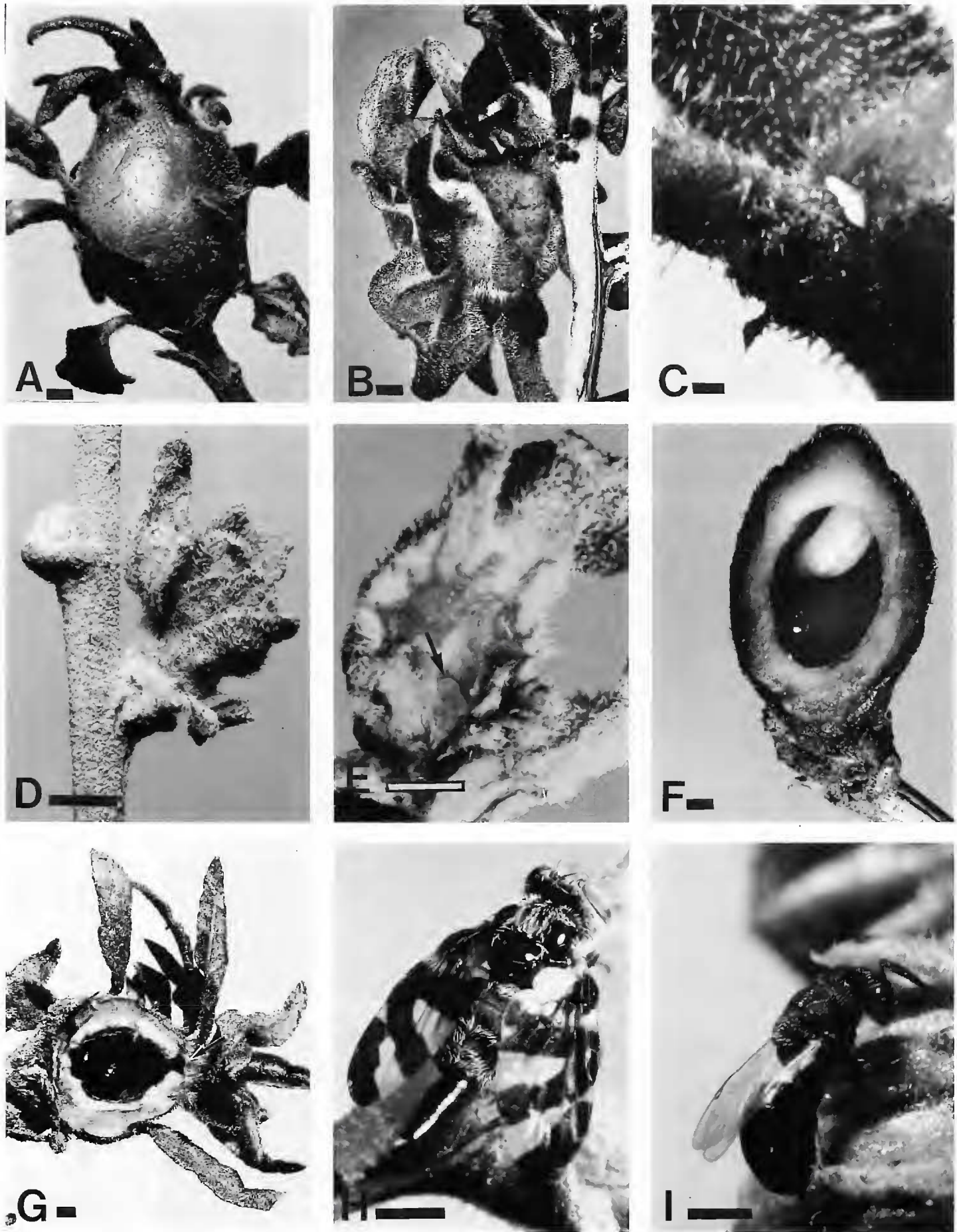
Figure 6. (A) gall of *P. stonei* on type host, *Viguiera laciniata*; (B) gall of *P. stonei* on *V. deltoidea* var. *parishii*; (C) cluster of three eggs laid in leaf axil on *V. laciniata*; (D) immature gall on *V. d.* var. *parishii*; (E) immature gall on *V. d.* var. *parishii* dissected to show first instar larva (arrow) in small cavity; (F) saggital section of gall on *V. laciniata* containing a third instar larva and puparium; (G) saggital section of gall on *V. laciniata* containing two puparia and showing the exit tunnel (arrow); (H) adult female of *P. stonei*; (I) Adult female of *Eurytoma* sp., the most common parasite of *P. stonei*. Bars = 1 mm.

galls (Fig. 6E) until rain stimulates plant regrowth in late-winter/early-spring, as described for *Procecidochares* sp. on *Ambrosia dumosa* (Gray) Payne by Silverman & Goeden (1980). Occasional late-summer rains also may stimulate a second annual flush of plant growth and host and fly reproduction (Silverman & Goeden 1980). A sample of 27 galls collected from *V. d.* var. *parishii* at Chino Canyon on 31 October 1991 yielded 25 dormant first instar larvae, 19 (86%) of which were found singly in galls. Of 22 galls collected from *V. laciniata* at Oriflamme Canyon in December 1989, 12 (55%) contained second or third instar larvae, and 10 (45%) held puparia (Fig. 6F). Larval growth proceeds rapidly through the second and third stadia as host-plant growth resumes. Of 260 galls collected in February 1990 and 1991, from both host species, four (2%) contained first instar larvae, eight (3%) had second instar larvae, 25 (10%) had third instar larvae, 234 (90%) contained puparia (Fig. 6G); 10 galls contained both larvae and puparia. Before pupariation, the third instar larva chews an exit tunnel in the gall wall out through the leafy apex (Fig. 6G—arrow), as reported by Silverman & Goeden (1980).

Puparia.—By March 1990 and 1991, 71 (88%) of 80 galls contained puparia (Fig. 6G); and flies had emerged from 38 (60%) of 64 of these puparia examined more closely. In April 1990, a sample of 46 galls from the Palms-to-Pines site contained only puparia, and flies had emerged from 46 (70%) of 66 puparia within them. Puparia were oriented with their cephalic ends toward the exit tunnels. In galls with more than one puparia, they were usually bound together with a thin, clear, oily liquid. Adults emerged from puparia held in vials during late February through mid-March.

Effects of Drought. — *Viguiera d.* var. *parishii* was common at the Palms-to-Pines site, but 4 years of drought had taken their toll, as only 10–40% (visual estimate) of each galled plant showed new growth. Most regrowth occurred on plants that grew at the bases of boulders or rocky outcrops and thus benefitted from additional water runoff. Eleven galled host-plants along a 500-m, east–west transect averaged 72 ± 10 cm in diameter and 50 ± 5 cm in height. Previous-years' galls, i.e., 2 or more years old, were found on all 11 plants and totalled 404, with the galls evenly distributed basally among the four quadrants (Table 1). Last-year's galls were found on eight of the 11 (72%) plants and totalled 44, with most concentrated in the southwest and southeast quadrants, and typically located half way up the stems. Current-years' galls were found only on four of the 11 (36%) plants and totalled only 16, with most concentrated in the southeast quadrant, and located distally half to two-thirds of the distance along the stems (Table 1). These data suggested that as water-stressed plants put on less new growth each year of the current drought, the numbers of galls also decreased commensurately.

A few *V. d.* var. *parishii* at each desert site remained relatively healthy because of their location along the driplines of boulders, as mentioned, or along paved roads, where rain runoff also gave them an added measure of water. By locating and ovipositing on these few relatively flush plants, at least a small population of *P. stonei* had survived the drought conditions. Larval development is a facultative process dependent on host-plant physiology (Freidberg 1984). Evidence suggests that in years of extreme drought, first-instar larvae may remain dormant for a year or more, until they die along with their hosts or incipiently infested parts of their hosts (Silverman & Goeden 1980). The galls sampled at Chino

Canyon in October, 1990, the fourth year of the drought, mentioned above, contained only dormant first-instar larvae.

Adults.—A total of 79 females and 76 males were reared from isolated puparia. Adults emerged during February and March 1990 and 1991, from galls collected on *V. laciniata* at Otay Valley and Otay Mesa. Females are proovigenic (Fig. 6H). Five, newly emerged females contained an average of 200 ± 12.1 (range 156–216) ova in their ovaries. Adults emerge ready to mate, and females oviposit shortly thereafter on the current branch growth.

The average longevity of 92 individuals obtained from *V. d.* var. *parishii* and *V. laciniata* individually caged was 19.5 days. Forty-one males lived an average of 24 days; five mated males lived an average of 23 days. Fifty-one females lived an average of 16 days; 12 mated females lived an average of 16 days, and 10 of those that were allowed to oviposit lived an average of 15 days. Death occurred an average of 5.5 days after they ceased oviposition. The greatest longevity recorded was 64 days for a male obtained from *V. laciniata* at Otay Mesa. Flies from Otay Mesa on average lived longer, i.e., 39 days for males, 20 days for females, and 30 days for all flies.

Wing Displays.—Adults of *P. stonei* are dark-bodied and have three dark, transverse bands on their hyaline wings (Fig. 6H). At rest, the wings are usually held parted at about 45°, with the wing blades supinated ca. 45°, such that their anal margins touch the sides of the abdomen at ca. 160°. The medial margin of the wings forms a straight line across the posterior margin of the body, and completes a triangle with the costal margins of the wings (Fig. 6H). From this position, the wings are synchronously and quickly extended forward and returned through 30° to 45° arcs. This motion is repeated several times in 1-sec bursts, which usually involve three repetitions. This general wing movement we call "enantion," a term derived from the Greek preposition meaning "against." This wing display is typical of *Procecidochares* (Headrick, unpublished data), all species of which have a similar habitus. Resting or grooming adults of *P. stonei* spontaneously displayed wing enantion; males also displayed enantion during courtship. Moreover, both sexes visually oriented to nearby movement by turning and facing the conspecific fly, predator, or other stimulus, and displaying rapid wing enantion. The male apparently uses wing enantion to further stimulate the female while gaining intromission (see below).

Males exhibited more variation in wing displays than did females, which only displayed enantion. Wing display intensity depended on the time of day and state of sexual excitment of the male. When a male approached a female for courtship, his wings vibrated very rapidly, appearing as a sustained blur. Males rarely showed asynchronous extension of their wings during courtship. The asynchronous display involved one wing extending slightly forward, then returning to its resting position, at which point the other wing similarly was extended. This wing movement was much slower than the rapid synchronous thrusts of enantion.

Grooming.—Adults used their hind legs to clean all sides of their abdomen, both sides of their wings, and the top of their thoraces. The hind legs were rubbed together beneath the abdomen for cleaning. The foretarsi were used to clean the head and also, were rubbed together for cleaning. The middle legs were used only to help clean the fore and hind legs. Females exerted their ovipositors occasionally

to clean the eversible membrane and aculeus with their hind tarsi and the distal parts of their hind tibia.

Feeding and Waste Excretion.—The mouthparts of both sexes pumped rapidly and nearly continuously, regardless of other activities. The female mouthparts pumped at about half the rate of the males. Adults readily drank water provided to them in cages and arenas.

Courtship.—Males faced females and began asynchronous wing displays, starting at two to three extensions per sec and increasing in speed to a blur as excitation of the males increased. Males trailed females while continuing their asynchronous wing displays. Females answered with only one type of display (i.e., synchronous wing extension without supination). When a male followed a female, he attempted to mount her by jumping onto her dorsum. Although females were able to escape the advances of a male by jumping away, males usually were able to grasp the females and hang on. Once the male had mounted, females did not try to escape.

Copulation.—The male positioned himself on a female with the claws of his foretarsi hooked basally around the costal veins of the females. His middle legs wrapped around her abdomen near her thorax, and his hind legs were brought underneath her abdomen near the base of the oviscape (= syntergosternite VII of Norrbom & Kim 1988). Non-virgin males raised the oviscape at a 45° angle by means of his hind legs; whereupon, the female in response immediately exerted her aculeus; he then held his terminalia against the oviscape apex and the epandrium received the aculeus. Next, the female fully exerted her ovipositor, an action that stretched the abdomen of the male to its limits. After a few minutes, the female relaxed and the male assumed a normal copulatory position with his forelegs on her abdomen near her thorax, his middle legs around her abdomen near the ovipositor, his hind legs on the substrate, and the epandrium held against the partially exerted, eversable membrane.

If the female did not exert her aculeus immediately, the male drummed his hind legs against the venter of her abdomen and ovipositor. If this did not elicit a response, he displayed wing enantion coupled with drumming. This behavior was usually followed by the female exerting her aculeus. The aculeus was held in place by the surstyli, with its tip raised, thus opening the ventral flap. The aedegus was then inserted through the ventral flap into the oviduct while the ovipositor was fully extended. As the ovipositor was slowly retracted, the aedeagus was further thrust into the oviduct by pulsations of the abdomen of the male. Mated pairs remained *in copula* from 20 min to 8 h, averaging about 2 h ($n = 13$), which was longer than averages of 1 h observed for *P. minuta* (Snow) (Headrick, unpublished data) and 30 min reported for *Procecidochares* sp. from *A. dumosa* (Silverman & Goeden 1980). To terminate copulation, the male turned 180°, and walked off the dorsum of the female and away from her while pulling his aedeagus out of her aculeus. Once free, the male groomed and recoiled his aedeagus, while the female also groomed herself. No post-mating activity other than grooming was observed.

On one occasion, a male of a pair that had mated 5 days earlier was observed trying to remount the same female. The male jumped on the female from the front and turned around on her back to gain access to the oviscape; however, she kept it covered with her wings so he could not reach down and grasp it with his

hind legs. He turned 360° twice while on top of her, and crawled down her side twice while trying to grasp her oviscape. He then moved back on top of her and tried to grasp her oviscape posteriorly with his hind legs. The female exerted her aculeus as if to initiate coitus, and the male fell off. He did not attempt to mount the female again.

Virgin males showed one of the few examples of naïve mating behavior reported among Tephritidae. During two separate trials, while a naïve male was on top of a female in the typical initial position, he began drumming with his hind legs against her oviscape without raising it. The female exerted on command, but she extended her aculeus so that the male couldn't move posteriorly far enough to engage the aculeus tip with his epandrium. This drumming by both males and exertions of the aculeus by both females continued for nearly an hour in each case, when finally each male successfully raised the oviscape and engaged the aculeus, thus gaining intromission.

Oviposition.—Oviposition trials were carried out in the field and laboratory with mated females from the above trials. Individual females were caged on branches of *V. laciniata* or *V. d.* var. *deltoidea* obtained from the University of California, Riverside, Botanic Garden. *Viguiera d.* var. *parishii* was unavailable locally. The variety *deltoidea* is found naturally only in Baja California (Shreve & Wiggins 1964). Females actively explored, and probed leaf axils of both test species immediately after being caged on plants in the field, or with freshly cut branches in the laboratory. When a female was ready to oviposit she turned away from the stem and pushed the tip of her deflexed ovipositor into the axil between a leaf base and stem (Fig. 6C). Except for a single group of two eggs laid near a branch tip, females always chose axils on current season's growth lower on branches near the main axis of the plant for oviposition. This corresponded with field data on gall positions on plants.

Natural Enemies.—At least four species of parasitic Hymenoptera emerged from puparia in rearing vials. A *Eurytoma* sp. (Eurytomidae) was the predominant parasitoid at all locations. This solitary, internal larval-pupal parasitoid was recovered from 300 puparia from all sample dates and locations (Fig. 6I). Nineteen individuals of a *Halticoptera* sp. (Pteromalidae) also were reared singly from puparia collected at Otay Valley and Otay Mesa in 1991. A *Tetrastichus* sp. (Eulophidae) was represented by 140 individuals recovered from 26 puparia from all locations except Otay Mesa. A single male of a *Spilochalcis* sp. (Chalcididae) was recovered from puparium from Mountain Springs. Five solitary, ectoparasitic torymid larvae, one of which had an internal hyperparasite, were found feeding on larvae of *P. stonei* in separate galls.

Host Range

Tauber & Tauber (1968) described the biology of *P. stonei,* which they had identified from a single, dead, teneral adult that had partly emerged from a gall on *Chrysothamnus viscidiflorus* (Hooker) Nuttall. At that time, several undescribed species of *Procecidochares* were identified as *P. stonei* or near (Silverman & Goeden 1980). However, the gall Tauber & Tauber (1968) described and illustrated is quite different morphologically from the galls described from the type host plant and type locality of *P. stonei* in the present paper. This gall also is radically different morphologically from those of a *Procecidochares* sp. on *A.*

dumosa (Silverman & Goeden 1980) and at least five additional species of *Procecidochares* currently under study by Goeden, Headrick & Teerink (unpublished data); at least two of these occur on another *Chrysothamnus* species, *C. nauseosus* (Pallen) Britton. It only has a very small central cavity and is largely composed of a series of overlapping, sessile, linear leaves (Tauber & Tauber 1968: figs. 1, 2), which is strongly reminiscent of certain cecidomyiid galls (Gagné 1989), and unlike any other tephritid gall (*Procecidochares* included) seen by RDG in California to date. In June, 1986, a sample of 62 galls from *C. viscidiflorus* like those first described by Tauber & Tauber (1968) were collected in Deep Spring Valley, Inyo County, dissected, and thoroughly examined by RDG (unpublished data). Unfortunately, they contained only empty puparia, but these were similar in size and color to those of the species of *Procecidochares* described by Tauber & Tauber (1968) (i.e., smaller, narrower, and partially pigmented dark brown, only a few completely black, unlike those of *P. stonei* described here). These data suggest that the species studied by Tauber & Tauber (1968) was not *P. stonei,* but rather the "*Procecidochares* sp. A" of Wangberg (1980), which Novak et al. (1967) reported as *P. minuta.*

Based on the present study, and published (Silverman & Goeden 1980) and unpublished field and laboratory studies of other *Procecidochares* in California (Goeden, Headrick, & Teerink, unpublished data), we suggest that the host records in Wasbauer (1972) for *P. stonei* from *Ambrosia dumosa, Corethrogyne filaginifolia* (Hooker & Arnott) Nuttall, and *Chrysopsis* (as *Heterotheca*) *villosa* (Pursh) Nuttall are misidentifications of other *Procecidochares* species. *Procecidochares stonei* apparently is restricted to *Viguieria* spp., which are found in a different tribe of Asteraceae than are *C. filaginifolia* and *C. villosa,* both in the Astereae.

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